Cretaceous Research 41 (2013) 55–64

Contents lists available at SciVerse ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Soft-shelled turtles (Trionychidae) from the Bissekty Formation (Late Cretaceous: late Turonian) of Uzbekistan: Shell-based taxa

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ARTICLE INFO

Article history:
Received 6 July 2012
Accepted in revised form 28 October 2012
Available online 30 November 2012

Keywords:
Turtles
Testudines
Assemblage
Middle Asia
Kazakhstan

ABSTRACT

In this paper we describe previously unpublished trionychid turtle material, consisting of numerous shell fragments, from the Late Cretaceous (late Turonian) Bissekty Formation of the Dzharakuduk locality in Uzbekistan. This material is assigned to two shell-based taxa: *Aspideretoides* cf. *riabinini* and "*Trionyx*" cf. *kansaiensis*. The material which cannot be confidently attributed to these two taxa is identified as Trionychidae indet. In addition to these shell-based trionychid taxa, the Dzharakuduk turtle assemblage includes two skull-based taxa of trionychids (*Khunnuchelys kizylkumensis* and Trionychini indet.). The trionychids from the Bissekty Formation are most similar to trionychids from the younger (Santonian – early Campanian) Bostobe Formation of Kazakhstan, represented by three shell-based taxa (*Aspideretoides riabinini*, *Paleotrionyx riabinini* and "*Trionyx*" *kansaiensis*), and one skull-based taxon (*Khunnuchelys* sp.). We provide an improved understanding of the subtle similarities and differences between four closely related Cretaceous turtle assemblages of Middle Asia and Kazakhstan.

1. Introduction

Trionychidae Gray 1825, or soft-shelled turtles, are a group of aquatic cryptodires (Meylan, 1987). The phylogeny and taxonomy of extinct species within this group are still not well understood (Meylan, 1987; Gardner et al., 1995; Karl, 1998; Joyce and Lyson, 2011). The lack of understanding is especially problematic for Cretaceous trionychids, which are important for understanding the early diversification and evolution of the family (Danilov and Vitek, 2012 provided a review of Cretaceous trionychids of Asia).

This paper continues a series of publications on Cretaceous trionychids of Asia (Danilov and Vitek, 2009; Vitek and Danilov, 2010, 2012; Danilov and Vitek, 2012) and is devoted to trionychids from the Late Cretaceous (late Turonian) Bissekty Formation of the Dzharakuduk (Dzharakuduk II; Nessov, 1997) locality in Uzbekistan (Fig. 1; see Vitek and Danilov (2010) for more details about geography).

The first report on trionychids from Dzharakuduk was published by Nessov (1985), who mentioned a "high-shelled big *Trionyx* 2" (Nessov, 1985:218) from that locality. More information about that trionychid was published later (Nessov, 1986). It was compared with a trionychid from "the Cenomanian of Sheichdzheili" (Khodzhakul Formation, Uzbekistan) and characterized as follows: "…trionychid from Dzharakuduk has a relatively high carapace; a longer nuchal bone; the callosities of the plastron were weaker and less spacious; the xiphiplastra were broad, curved and pitted on the outside" (Nessov, 1986:10). In the same publication, skull characters of that trionychid were listed and its braincase and maxilla were figured (Nessov, 1986: 10, figs. 9, 14). Additional trionychid skull material was figured in the next publication (Nessov, 1987: figs. 8, 9). Some of that skull material was later used in the description of *Khunnuchelys kizylkumensis*, a skull-based taxon from Dzharakuduk (Brinkman et al., 1993). In addition, shell material which likely belonged to that species, as well as shell material that probably belonged to a second trionychid with slender jaws from this locality was mentioned by Brinkman et al. (1993). Later, two trionychid taxa (*Khunnuchelys kizylkumensis* and *Palaeotrionyx* sp.) in the Dzharakuduk assemblage were listed and figured (Nessov, 1997). In addition to some previously illustrated material, two shell fragments which were referred to *Palaeotrionyx* sp. (Nessov, 1997:pl. 40, figs. 3, 4). More information about skull material of the second, slender-jawed trionychid from Dzharakuduk, which was determined as Trionychini indet, was reported by Danilov (2007). A probable association of that skull material with shell material from Dzharakuduk which was diagnostic for *Aspideretoides* was suggested by Danilov and Vitek (2009, 2012). We also mentioned the previously reported shell material from Dzharakuduk that probably belonged to *Khunnuchelys kizylkumensis*. In addition to those material-based papers about Dzharakuduk trionychids, some

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http://dx.doi.org/10.1016/j.cretres.2012.10.003

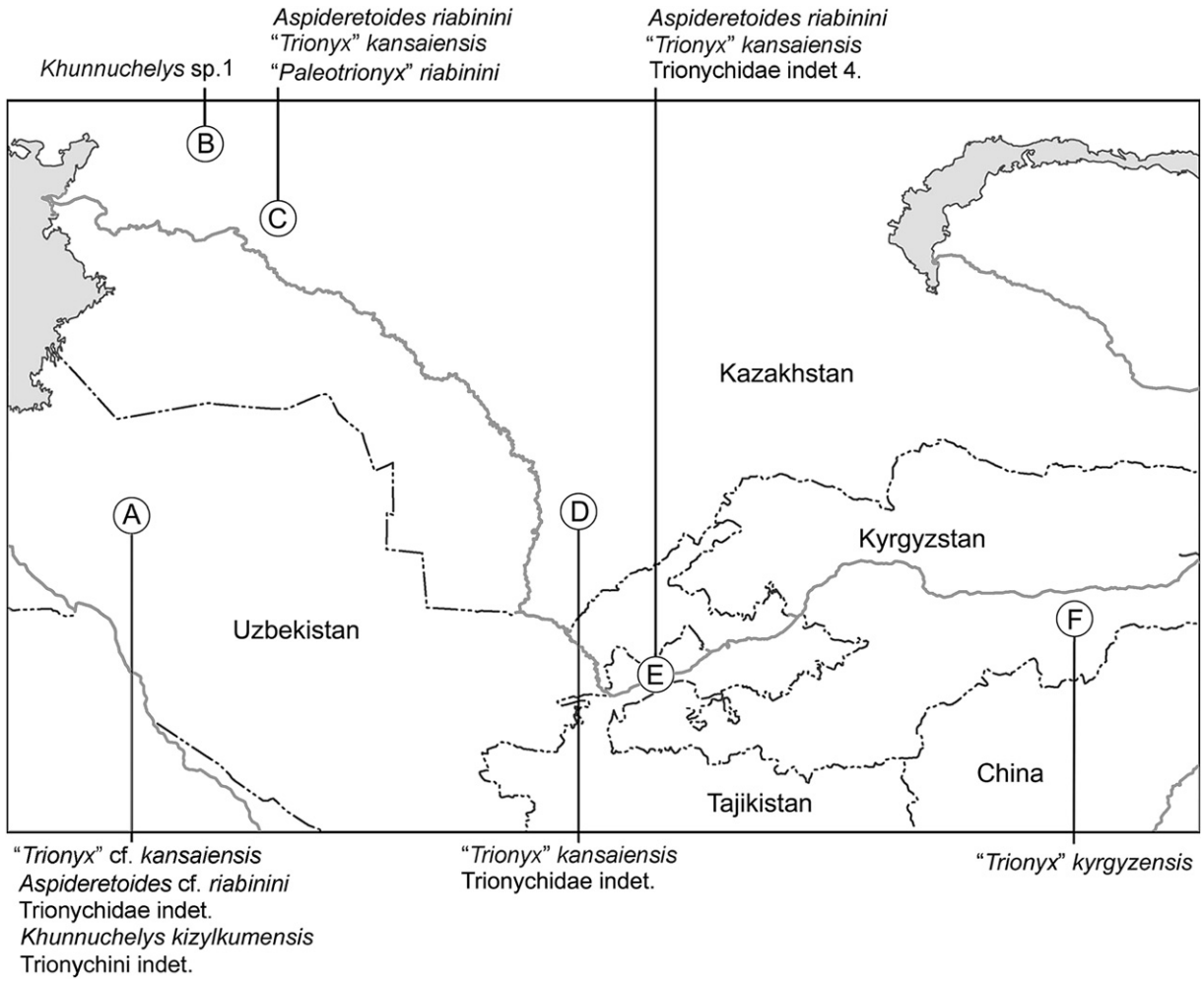

Fig. 1. Map showing main localities of Late Cretaceous trionychids in Middle Asia and Kazakhstan. A, Dzharakuduk. B, Baybishe. C, Shakh Shakh. D, Kyrkkuduk I. E, Kansai. F, Kylodzhun (modified from Vitek and Danilov (2010, fig. 2; 2012, fig. 1); see those publications for data on localities).

authors suggested different systematic attributions for the taxa (see Danilov and Vitek, 2012 for lists of synonymies).

Here we describe previously unpublished trionychid turtle material from Dzharakuduk. The material consists of numerous shell fragments. It is assigned to two shell-based taxa, *Aspideretoides* cf. *riabinini* (Kuznetsov and Chkhikvadze, 1987) and "*Trionyx*" cf. *kansaiensis* Vitek and Danilov, 2010. Material that cannot be confidently attributed to these two taxa is considered as Trionychidae indet. The description of the unpublished material of the skull-based taxa and discussion of possible skull-shell associations based on size differences and similarities between Asian trionychine forms and North American specimens of *Aspideretoides* will be published elsewhere. Comparison of the described shell-based trionychid taxa was made primarily with *Aspideretoides riabinini* and "*Trionyx*" *kansaiensis* from Kansai and Shakh Shakh localities (Vitek and Danilov, 2010), as well as with other trionychid taxa from the Cretaceous of Asia (see Danilov and Vitek, 2012). Anatomical terminology follows Meylan (1987), Gardner and Russell (1994), and Karl (1999).

Institutional Abbreviations—**ZIN PH**, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

2. Systematic paleontology

Testudines Batsch, 1788
Cryptodira Cope, 1868
Trionychidae Gray, 1825
Trionychinae Gray, 1825
Trionychini Gray, 1825
Aspideretoides Gardner, Russell, and Brinkman, 1995

Content. Four species: *Aspideretoides allani* (Gilmore, 1923); *A. beecheri* Hay, 1905; *A. foveatus* (Leidy, 1856) (type species); *A. riabinini* (Kuznetsov and Chkhikvadze, 1987).

Diagnosis. See Gardner et al., 1995.

Remarks. *Aspideretoides splendidus* (Hay, 1908), placed in *Aspideretoides* by Gardner et al. (1995), was recently moved to the genus *Axestemys* (Hay, 1899) (Vitek, 2012). *Eugenichelys robertemryi* Chkhikvadze, 2008, tentatively referred to *Aspideretoides* by Danilov and Vitek (2012), was shown to be a junior synonym of *Axestemys byssina* Cope, 1872 (Vitek, 2012).

Aspideretoides cf. *riabinini* (Kuznetsov et Chkhikvadze, 1987)

Palaeotrionyx sp.: Nessov, 1997:145, pl. 40, figs. 3, 4.
Aspideretoides sp. (part.): Danilov and Vitek, 2009:54; Danilov and Vitek, 2012:425.

Referred material. ZIN PH 404/108, ZIN PH 429/108, ZIN PH 438/108, ZIN PH 445/108, ZIN PH 458/108, and ZIN PH 460/108, partial

nuchal; ZIN PH 650/108, nuchal and costal 1 fragment; ZIN PH 83/108, costal 1; ZIN PH 76/108, and ZIN PH 95/108, partial costal 1; ZIN PH 673/108, costal 5; ZIN PH 374/108, costal 7; ZIN PH 378/108, partial costal 7; ZIN PH 72/108, partial costal 7 and 8; ZIN PH 78/108, ZIN PH 384/108, costal 8; ZIN PH 819/108, costal; ZIN PH 636/108, ZIN PH 641/108, ZIN PH 642/108, ZIN PH 685/108, partial costal; ZIN PH 232/108, neural 1; ZIN PH 289/108, partial hexagonal neural; ZIN PH 303/108, pentagonal neural; ZIN PH 317/108, tetragonal neural; ZIN PH 43/108, partial medial hyoplastron; ZIN PH 21/108, ZIN PH 837/108, partial hyoplastron; ZIN PH 4/108, ZIN PH 6/108, partial hypoplastron; ZIN PH 33/108, ZIN PH 1136/108, partial xiphiplastron.

Locality, Horizon, and Age. Dzharakuduk (= Dzharakuduk II; Nessov, 1997), Central Kizylkum Desert, Navoi Viloyat (district), Uzbekistan; Bissekty Formation, late Turonian.

Description. Shell. A reconstruction (Fig. 2A), with scale based on the largest identifiable partial nuchal (ZIN PH 458/108; Fig. 3A), is approximately 32 cm long, smaller than *Aspideretoides riabinini* specimens from Kansai and Shakh Shakh (Vitek and Danilov, 2010). Material from several smaller carapaces (Fig 2B) is also present. Some of this material, such as an isolated costal 6 (ZIN PH 673/108; Fig. 3B) indicate a carapace as small as 15 cm. Although there is a wide range of sizes among the catalogued material, there are no distinct size divisions or other characters that clearly indicate sexual dimorphism. Larger carapaces are approximately circular. Smaller carapaces are more oval, with long, uncallosified rib ends.

The anterior margin is slightly emarginated. In some cases, it may be more emarginated than nuchals from Kansai (ZIN PH 438/108; Fig. 3C, D). The posterior margin is straight with a variable medial notch, similar to *Aspideretoides riabinini*. The lateral margin ranges from straight to scalloped. Sculpturing consists of thin, intersecting ridges that form a net-like pattern, similar to the sculpturing of *Aspideretoides riabinini*. In addition, some specimens (e.g., ZIN PH 373/108; Fig. 3E) show a pattern of thicker, secondary ridges that tend to run antero-posteriorly. Such ridges are generally found on smaller individuals, and may be reflective of ontogeny rather than of differences between species.

Nuchal. A reconstruction based on a partial nuchal (ZIN PH 438/108) is about five times wider than long, within the range of ratios seen in *Aspideretoides riabinini*. The extent of the sculptured callosity on the nuchal is generally, but not always, correlated with size; smaller nuchals tend to not be callosified anteriorly and laterally (ZIN PH 404/108, Fig. 3F) , but larger nuchals tend to show a slightly smaller uncallosified area (ZIN PH 458/108), or none at all (ZIN PH 438/108). This variation is considered ontogenetic because it appears to be related to size. Nuchal and costal 1 fragments preserving the posteriomedial margin variably show postnuchal fontanelles (ZIN PH 76/108, ZIN PH 429/108, ZIN PH 445/108, ZIN PH 460/108; Fig. 3G–J). The costiform processes are united and the position of the two depressions on the visceral side of the nuchal indicate that the first body vertebra contacted the middle of the nuchal (ZIN PH 438/108). An extensive portion of the posterolateral edge of the nuchal extends into costal 1 (ZIN PH 650/108; Fig. 3K).

Neurals. The presence of a preneural is evident from the medial margin of costal 1 (ZIN PH 95/108; Fig. 3L) and from the anterior emargination of neural 1 (ZIN PH 232/108; Fig. 3M). In this character it is similar to *Aspideretoides riabinini*, "*Aspideretes*" *maortuensis* Yeh, 1965, "*Trionyx*" *kyrgyzensis* Nessov, 1995, and *Sinamyda fuchienensis* (Yeh, 1974). Here, the preneural is considered separate from costal 1 and is not included in the neural count, unlike Meylan's (1987) terminology.

The medial margins of costals 7 (ZIN PH 373/108 and ZIN PH 374/108; Fig. 3N) indicates that there were seven neurals along the midline. In addition to the octagonal neural 1, there are several isolated hexagonal neurals (e.g., ZIN PH 239/108; Fig. 3O), tetragonal neurals (e.g., ZIN PH 317/108; Fig. 3P), and reduced pentagonal neurals (e.g., ZIN PH 303/108; Fig. 3Q) in the collection. The medial margin of isolated costals 2 or 3 (ZIN PH 819/108; Fig. 3R) indicates that the first five neurals were hexagonal, with short posterolateral sides. The medial margin of costal 6 (ZIN PH 673/108) indicates a tetragonal neural 6. After that, neural 7 is reversed, with short anterolateral sides. *Aspideretoides riabinini* also sometimes shows reversal at neural 6, or at the adjacent neural 5. In addition, "*Aspideretes*" *maortuensis* has an identical reversal pattern, although it has eight neurals in total, not seven. "*Aspideretes*" *alashanensis* Yeh, 1965 has seven neurals, but a reversal at neural 5.

Costals. Most costals 7 and 8 material from Dzharakuduk indicates that this species had eight costals, with costals 8 reduced and eye-shaped (ZIN PH 78/108, ZIN PH 384/108; Fig. 3S, T). However, there is also a small costal 7 (ZIN PH 72/108; Fig. 3U, V) that reaches the midline and includes both the seventh and eighth costal ribs, indicating that in some individuals costal 8 was lost altogether. *Aspideretoides riabinini*, *"Aspideretes" alashanensis*, "*Amyda*" *menneri* Chkhikvadze and Shuvalov, 1988, "*Amyda*" *orlovi* Khosatzky, 1976, and possibly *Sinamyda fuchienensis* also have reduced, but present, costals 8. Costals 7 meet partially and costals 8 meet fully at the midline. Costals 7 and 8 make up the posterior margin of the carapace.

Few complete costals are preserved, and only one of those complete costals has an expanded lateral margin. Therefore, it is unclear if any costals have a characteristically expanded lateral margin or if the character is variable. A complete costal 1 has lateral margin shorter than the medial margin (ZIN PH 83/108; Fig. 3W). A complete costal 6 (Fig. 3B) has a long, expanded lateral margin. Only one costal fragment shows that another costal overlaid it (ZIN PH 636/108; Fig. 3X), but it is unclear which costal this fragment represents and whether or not overlap is variable. Unlike material of *Aspideretoides riabinini* from Kansai, costals 6 of this species do not appear to have overlain costals 7 at the suture between the two bones.

The length of the free rib ends varies with size and, by inference, with ontogeny. The ribs of smaller, probably younger, specimens extend far beyond the callosified carapace and can make up as much as a third of total costal width (ZIN PH 819/108). In larger, probably older, specimens, the ribs only extend a few millimetres from the edge of the carapace (ZIN PH 685/108; 3Y, Z). The lateral margin ranges from concave (ZIN PH 685/108) to vertical (ZIN PH 642/108, 3AA, BB) to bevelled (ZIN PH 641/108, 3CC, DD). Such a wide range of variation was not seen in the Kansai material, but it still within the limits of intraspecific variation for extinct species of trionychid (Gardner and Russell, 1994).

Plastron. No epiplastra or entoplastra could be identified among the Dzharakuduk material. The hyo- and hypoplastra are covered in sculptured callosities (Fig. 2C) In smaller specimens, the callosity is more reduced and more likely to leave lateral and medial processes exposed. The xiphiplastra also are covered in a sculptured callosity, meaning that there were at least four callosities on the plastron, although the total number of callosities is unknown. Sculpturing is similar to the type seen on the carapace, but the ridges are often less narrow and are more likely not to intersect, and instead form a pattern of separate ridges rather than a net-like pattern. Distinguishing plastral elements between the two shell-based species of trionychid present in Dzharakuduk based on sculpturing is impossible, and several elements that may belong to this species are described under Trionychidae indet.

Hyoplastra and hypoplastra. The hyoplastra and hypoplastra are not fused, even in the largest specimens identified. There are no sutures at the medial margin of either the hyoplastron or

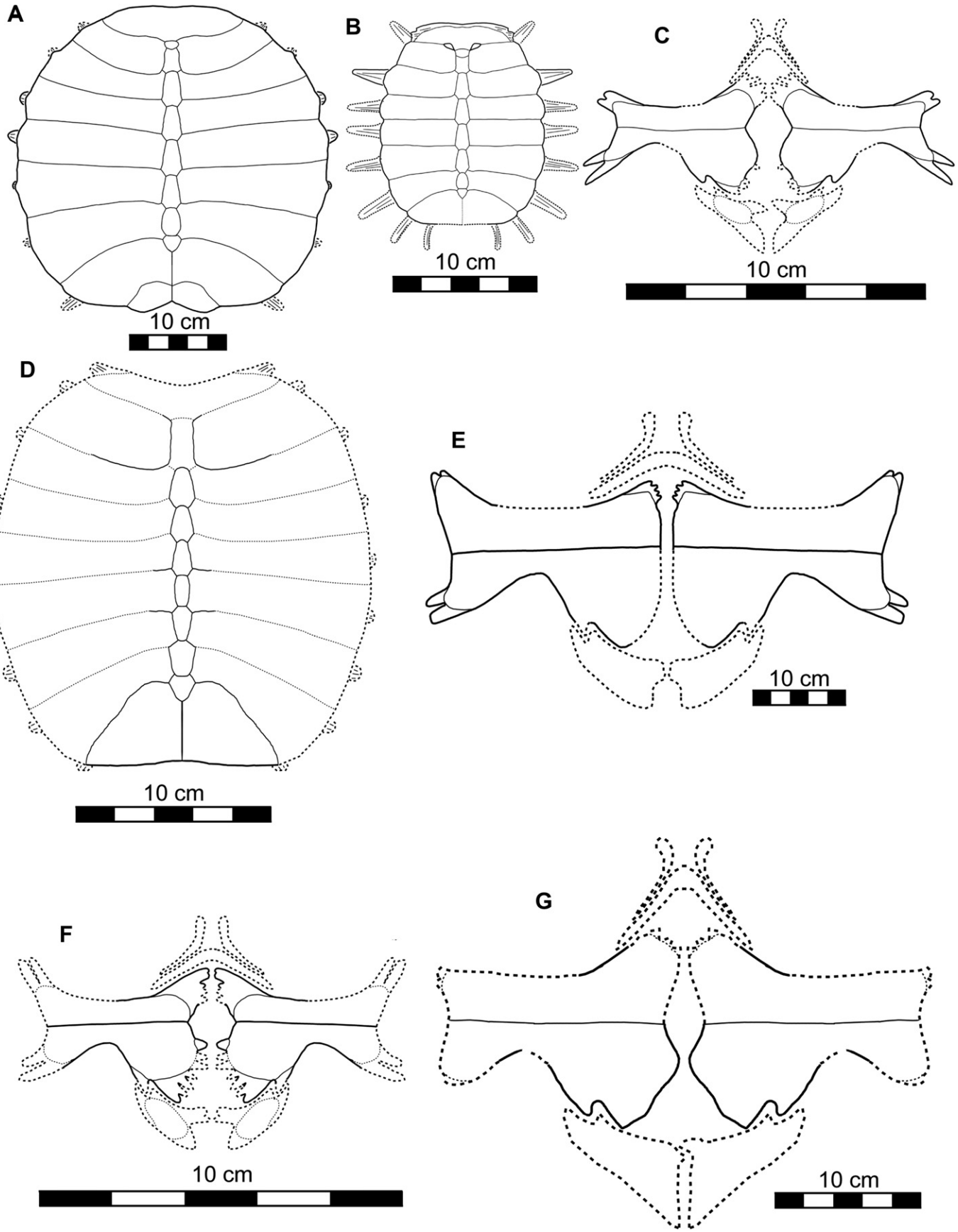

Fig. 2. Reconstructions of shells of trionychids from Dzharakuduk. A, adult carapace; B, juvenile carapace; C, plastron of *Aspideretoides* cf. *riabinini*. D, carapace, E, adult plastron, and F, juvenile plastron of "*Trionyx*" cf. *kansaiensis*. G, plastron based on material referred to Trionychidae indet.

Fig. 3. *Aspideretoides* cf. *riabinini* specimens from Dzharakuduk. A, ZIN PH 458/108, partial nuchal; B, ZIN PH 673/108, costal 6; C, anterior and D, visceral view of ZIN PH 438/108, partial nuchal; E, ZIN PH 373/108, costal 7; F, ZIN PH 404/108, partial nuchal; G, ZIN PH 76/108, partial costal 1; H, ZIN PH 429/108, partial nuchal; I, ZIN PH 445/108, partial nuchal; J, ZIN PH 460/108, partial nuchal; K, ZIN PH 650/108, partial nuchal and costal 1; L, ZIN PH 95/108, partial costal 1; M, ZIN PH 232/108, neural 1; N, ZIN PH 374/108, costal 7; O, ZIN PH 239/108, neural; P, ZIN PH 317/108, neural; Q, ZIN PH 303/108, neural; R, ZIN PH 819/108, costal; S, ZIN PH 78/108, costal 8; T, ZIN PH 384/108, costal 8; U, dorsal and V, visceral view of ZIN PH 72/108, costal 7; W, ZIN PH 83/108, costal 1; X, ZIN PH 636/108, partial costal; Y, lateral and Z, dorsal view of ZIN PH 685/108, partial costal; AA, lateral and BB, dorsal view of ZIN PH 642/108, partial costal; CC, lateral and DD, dorsal view of ZIN PH 641/108, partial costal; EE, ZIN PH 42/108, medial hyoplastron fragment; FF, ZIN PH 21/108, lateral hyoplastron fragment; GG, ZIN PH 4/108, medial hypoplastron fragment; HH, ZIN PH 837/108, medial hypoplastron fragment; II, ZIN PH 6/108, medial hypoplastron fragment; JJ, ZIN PH 33/108, partial xiphiplastron; KK, external and LL, visceral view of ZIN PH 1136/108, partial xiphiplastron.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
10 cm

hyoplastron, indicating that these elements did not meet at the midline. The length of the plastral bridge ranges from one-half to three-quarters the maximum hypoplastral length, similar to *Aspideretoides riabinini*.

The callosity on the medial hyoplastral lobe (ZIN PH 42/108; Fig. 3EE) extends anteriorly to cover most of the processes, unlike the other species from Dzharakuduk and *"Trionyx" kansaiensis* in which the processes are left exposed. The medial hyoplastral processes are not preserved. The bridge and lateral lobe of the hyoplastra are relatively flat and parallel to the suture (ZIN PH 21/108; Fig. 3FF), like in *Aspideretoides riabinini*.

The medial lobe of the hypoplastron (ZIN PH 4/108, ZIN PH 6/108, ZIN PH 837/108; Fig. 3GG, HH, II) shows a pattern of emargination similar to *A. riabinini*. The medial lobes are divided into an anterior group and a posterior group. The posterior group includes the process that articulates with the xiphiplastron. Between the hyoplastral-hypoplastral suture and the anterior group of processes there is one weak emargination, then between the first and second groups of processes there is a second emargination. This pattern was observed in all attributed medial hypoplastral fragments. However, it is possible that these emarginations disappear in much older specimens.

Xiphiplastron. A sculptured callosity covers much or all of two different xiphiplastral fragments (ZIN PH 33/108, ZIN PH 1136/108, Fig. 3JJ–LL). In the posterior fragment (Fig. 3KK), the callosity covers both the posterior and medial processes as well as the gap between them, leaving no emargination.

Trionychinae incertae sedis

"*Trionyx*" cf. *kansaiensis* Vitek and Danilov, 2010

Referred material. ZIN PH 98/108, partial costal 1; ZIN PH 632/108, partial costal 7 and 8; ZIN PH 391/108, costal 8; ZIN PH 1133/108, partial costal; ZIN PH 247/108, hexagonal neural; ZIN PH 283/208, partial hexagonal neural; ZIN PH 182/108 pentagonal neural; ZIN PH 20/108, ZIN PH 37/108, ZIN PH 39/108, ZIN PH 1100/108, partial hyoplastron; ZIN PH 9/108, ZIN PH 23/108, ZIN PH 841/108, partial hypoplastron; ZIN PH 31/108, ZIN PH 34/108, partial xiphiplastron.

Locality, *Horizon*, *and Age*. Dzharakuduk (= Dzharakuduk II; Nessov, 1997), Central Kizylkum Desert, Navoi Viloyat (district), Uzbekistan; Bissekty Formation, late Turonian.

Description. Shell. Very little shell material is attributable to this taxon. It is possible that this trionychid was rare within the turtle fauna of Dzharakuduk, and that little material was ever preserved. It is also possible that more material from this species may have been collected, but is unrecognizable due to the nature of preservation. Most of the trionychid fossils collected from Dzharakuduk are small and fragmentary. Sculpturing on attributable elements is similar to *"Trionyx" kansaiensis*, and consists of a pattern of wide, rounded ridges that rarely cross each other or form pits (Vitek and Danilov, 2010).

A loose reconstruction is based on the elements preserved, as well as on the reconstruction of "*Trionyx*" *kansaiensis* from Kansai (Fig. 2D). The size of the reconstruction based on material from Dzharakuduk ranges widely. The largest complete carapace element, an eighth costal (ZIN PH 391/108; Fig. 4A) indicates that the carapace was only about 22 cm long, much smaller than "*Trionyx*" *kansaiensis* and smaller than the other type of trionychid in Dzharakuduk. However, a large fragment of the lateral hypoplastron (ZIN PH 23/108; Fig. 4B) indicates that the plastron (Fig. 2E) reached a length of approximately 34 cm. A complementary carapace could have been about 46 cm long. This size is still smaller than both *Aspideretoides riabinini* and "*Trionyx*" *kansaiensis*, but larger than the other species present in Dzharakuduk. A fragment of the medial hypoplastron (ZIN PH 9/108; Fig. 4C) belonged to a small trionychid, probably only about 10 cm long. Whether or not the large range in size represents sexual dimorphism, intraspecific variation, or ontogenetic variation is unknown, although the latter two are probable based on other characteristics.

The shape of the carapace is unknown due to the lack of material. Furthermore, no nuchal fragments could be confidently attributed to this species. Whether or not this species had the characteristically strong anterior nuchal emargination of "*Trionyx*" *kansaiensis*, as well as other nuchal characteristics, is unknown.

Neurals. No preneural was found in the Dzharakuduk material that could be attributed to this species. In addition, the medial margin of costal 1 (ZIN PH 98/108; Fig. 4D) gives no indication that a preneural was present. The medial margins of costals 7 and 8 (ZIN PH 632/108; Fig. 4E) indicate that the final, reduced neural contacted costals 7 and 8. Given this arrangement, the carapace probably had eight neurals in total. Two hexagonal neurals and a reduced, pentagonal neural are preserved (ZIN PH 232/108, ZIN PH 283/108, ZIN PH 182/108; Fig. 4F–H). The orientation of the final neural indicates that it was reversed – that is, that the anterolateral sides were short in comparison to the posterolateral sides. Although no complete costals are preserved that would indicate where neural reversal occurred along the midline, a medial fragment of a costal (ZIN PH 1133/108; Fig. 4I) indicates that a tetragonal neural was present that would have preceded a reversed neural that had short anterolateral sides.

Costals. The carapace had eight costals, although only parts of costals 1, 7, 8, and costal fragments of uncertain position can be attributed to this species. The medial margin of costal 1 is preserved. The anteromedial margin has a suture for contact with the nuchal without postnuchal fontanelles. Costal 8 (ZIN PH 391/108) is unreduced. This arrangement is similar to "*Trionyx*" *kansaiensis*, and "*Trionyx*" *kyrgyzensis*. There is no depression on costals 8 for contact with the ilia. Only costals 8 met partially at the midline. Although costals 8 probably made up most of the posterior margin of the carapace due to their large relative size, they may not have made up the entirety. The posterior margin was probably straight, without a notch. No lateral costal margins with ribs are preserved (the rib of costal 8 crosses over onto costal 7 and the lateral end of the rib is therefore not preserved). The length of the rib ends, and whether they extended from the carapacial margin is unknown.

Plastron. No epiplastra or entoplastra could be identified among the Dzharakuduk material. The hyoplastron, hypoplastron, and xiphiplastron are covered in callosities, indicating that the plastron had at least four callosities (Fig. 4B, C, O, P). The xiphiplastral callosities lack sculpturing. The extent of the callosities varies with size. Larger specimens have a more extensive callosity, and smaller specimens have a less extensive callosity. Sculpturing is similar to carapacial sculpturing, but at smaller sizes the sculpturing closely resembles the sculpturing of the other species present in

Fig. 4. "*Trionyx*" cf. *kansaiensis* specimens from Dzharakuduk. A, ZIN PH 391/108, costal 8; B, ZIN PH 23/108, lateral hypoplastron fragment; C, ZIN PH 9/108, medial hypoplastron fragment; D, ZIN PH 98/108, partial costal 1; E, ZIN PH 632/108, partial costals 7 and 8; F, ZIN PH 232/108, partial neural; G, ZIN PH 283/108, neural; H, ZIN PH 182/108, neural; I, ZIN PH 1133/108, partial costal; J, ZIN PH 37/108, partial medial hyoplastron; K, ZIN PH 39/108, partial medial hyoplastron; L, ZIN PH 841/108, partial medial hyoplastron; M, ZIN PH 1100/108, partial medial hyoplastron; N, ZIN PH 20/108, partial lateral hyoplastron; O, ZIN PH 31/108, partial xiphiplastron; P, ZIN PH 34/108, partial xiphiplastron.

Dzharakuduk and material is not distinguishable based on sculpturing alone.

Hyo- and hypoplastra. The hyo- and hypoplastron are not fused together. There is no suture along the midline of either the hyo- or hypoplastron to indicate that they met along the midline. The plastral bridge length is just over half the maximum hypoplastral length.

The callosity on the medial hyoplastral lobe (ZIN PH 37/108, ZIN PH 39/108, ZIN PH 841/108, ZIN PH 1100/108; Fig. 4J–M) does not extend anteriorly to cover the medial hyoplastral processes, unlike *Aspideretoides riabinini* or *Aspideretoides* cf. *riabinini*. Instead, the extent of the callosity remains the same relative length as its extent on the hyoplastral bridge, similar to "*Trionyx*" *kansaiensis*. One medial fragment (ZIN PH 37/108) has four medial processes. The processes on the other fragments are not preserved, and the number of medial hyoplastral processes may be variable. The lateral lobe of the hyoplastron (ZIN PH 20/108; Fig. 4N) is more strongly angled and significantly longer than the medial lobe.

Only one small medial hypoplastral fragment (ZIN PH 9/108, Fig. 4C) could be confidently assigned to this species. The medial margin of the callosity is circular, and several medial processes extend beyond the callosified margin, without emargination or differentiation of the processes into groups. This arrangement is similar to "*Trionyx*" *kansaiensis* and "*Aspideretes*" *maortuensis*. The single lateral hypoplastral fragment (ZIN PH 23/108, Fig. 4B) has a much more extensive callosity that covers all but 2 cm of the lateral processes. Neither the contact with the hyoplastron nor the entire lateral margin is preserved in this fragment.

Xiphiplastron. The callosity on the xiphiplastra (ZIN PH 31/108, ZIN PH 34/108, Fig. 4O, P) lacks sculpturing entirely. The lateral margin is straight, except for the curved anterior processes that articulate with the hypoplastron. Although the processes grow to cover nearly the entirety of the processes, an emargination remains between the posterior and medial processes. In the overall shape, as well as the lack of sculpturing, on the callosities, these xiphiplastra closely resemble the xiphiplastron described from Kansai, as well as that from Kyrkkuduk (Vitek and Danilov, 2010, 2012).

Trionychidae indet.

Referred material. ZIN PH 449/108, ZIN PH 465/108, partial nuchal; ZIN PH 233/108, neural 1; ZIN PH 53/108, partial hyoplastron?; ZIN PH 13/108, ZIN PH 16/108, ZIN PH 17/108, ZIN PH 348/108, ZIN PH 352/108, ZIN PH 360/108, partial hypoplastron.

Nuchal. Two nuchals (ZIN PH 449/108, ZIN PH 465/108; Fig. 5A, B) differ from the others identified from Dzharakuduk. Both preserve the posterolateral suture, where they appear to interlie the first costal. The lateral part of the nuchal callosity is shorter anterolaterally and ends in a sharper point than the callosities of the nuchals referred to *Aspideretoides* cf. *riabinini*. At the anterior edge of the nuchal there is a large uncallosified area, but the edge is broken and it is unclear how far this area extends. It is possible that these fragments belong to "*Trionyx*" cf. *kansaiensis* described above. It is also possible that these fragments represent intraspecific variation of the *Aspideretoides* cf. *riabinini*. The medial part of these nuchals, which would help decide which species these fragments belong to, is not preserved.

Neural. An elongated neural 1 (ZIN PH 233/108; Fig. 5C) that allows no space for a preneural was collected from Dzharakuduk. The sculpturing resembles *Aspideretoides riabinini*, but this species is previously known only with a preneural. It may be that the neural belongs to *"Trionyx"* cf. *kansaiensis* and that, like "*Trionyx*" *kansaiensis*, the sculpturing of smaller individuals resembles that of larger individuals of *Aspideretoides riabinini* (Vitek and Danilov, 2010). Alternately, the neural may belong to a third, previously unrecognized species of trionychid from Dzharakuduk.

Hyoplastron. A single element (ZIN PH 53/108; Fig. 5D, E) was found that is difficult to attribute to any element, much less to any

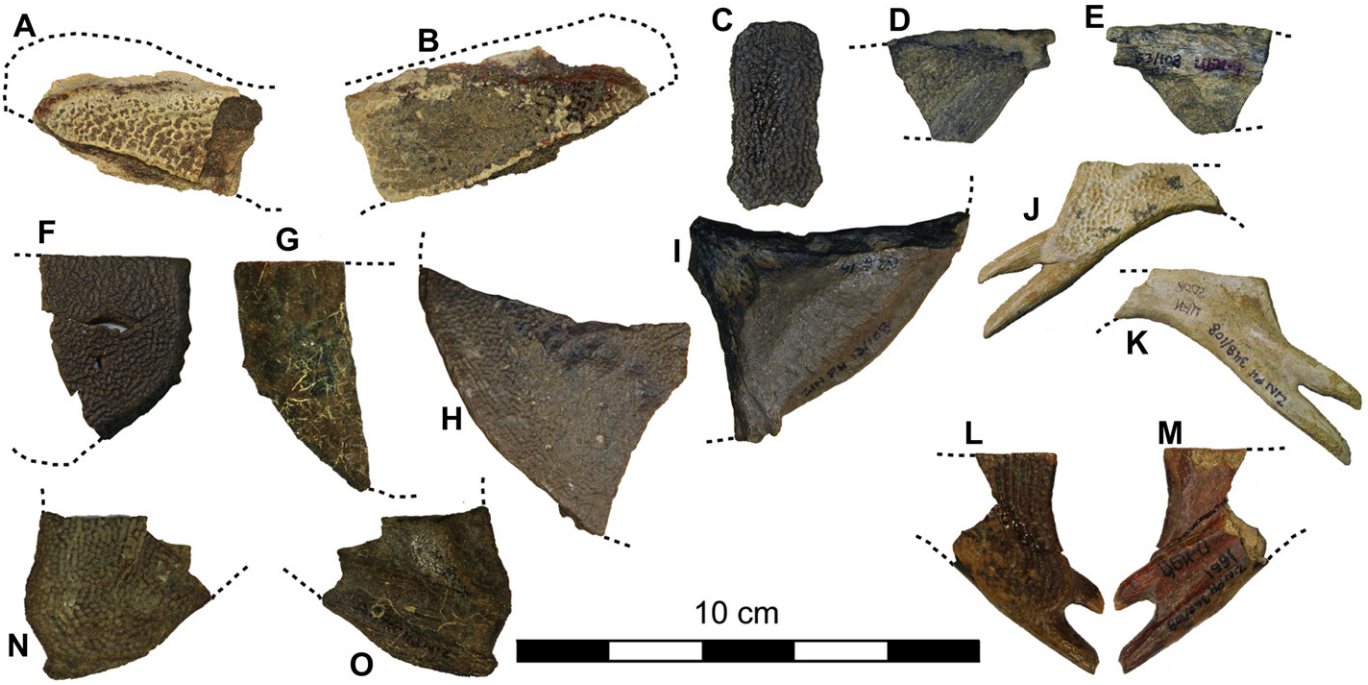

Fig. 5. Trionychidae indet. specimens from Dzharakuduk. A, ZIN PH 449/108, partial nuchal; B, ZIN PH 465/108, partial nuchal; C, ZIN PH 233/108, neural 1; D, external and E, visceral view of ZIN PH 53/108, partial lateral hyoplastron; F, ZIN PH 16/108, partial medial hypoplastron; G, ZIN PH 17/108, partial medial hypoplastron; H, external and I, visceral view of ZIN PH 13/108, partial medial hypoplastron; J, external and K, visceral view of ZIN PH 348/108, partial lateral hypoplastron; L, external and M, visceral view of ZIN PH 360/108, partial lateral hypoplastron; N, external and O, visceral view of ZIN PH 352/108, partial lateral hypoplastron.

species. It preserves two processes, similar to the lateral processes of the hyo- and hypoplastra of most trionychids. However, the callosity covering it is very extensive, extending far beyond what would be the hyo- or hypoplastral bridge and almost entirely covering the processes. It is tentatively identified as a lateral hyoplastron. As mentioned in the descriptions above, sculpturing is not a useful criterion here in the distinction between the two species. Whatever species to which it belongs develops extensive plastral callosities, not as extensive as in some Plastomenidae Hay, 1902, but more so than the material currently assigned to either species.

Hypoplastron. Three medial hypoplastron fragments are assigned to Trionychidae indet. All three are extensively callosified. The callosities of two of the fragments (ZIN PH 16/108, ZIN PH 17/108; Fig. 5F, G) cover all but 1–2 mm of the medial hypoplastral processes. The callosity of the third (ZIN PH 13/108; Fig. 5H, I) extends past the processes. All three fragments indicate differentiated groups of hypoplastral processes, similar to the *Aspideretoides riabinini*-type material described above, but are lacking clear emarginations. It may be that the emarginations are lost in large specimens, as mentioned previously. On the other hand, it could be that arrangement of the medial processes is a variable character within species, and that these fragments are more well-developed specimens of "*Trionyx*" cf. *kansaiensis* described above.

Three medial hypoplastral fragments are preserved that show the development of the lateral hypoplastra. The first (ZIN PH 348/108; Fig. 5J, K) resembles the pointed hypoplastra of *Aspideretoides riabinini*. The second (ZIN PH 360/108; Fig. 5L, M) has a much rounder point that covers much more of the lateral hypoplastral processes. The third (ZIN PH 352/108; Fig. 5N, O) is the most callosified. The processes are almost entirely covered and the posterolateral margin is nearly circular, then straightens out anterolaterally. Although extensive, these specimens are still not as extensively callosified as the Trionychidae indet. 5 from the Maastrichtian of Mongolia (Danilov and Vitek, 2012), and are closer to the hypoplastra of "*Trionyx*" *kansaiensis*. These specimens are much smaller than both the Kansai material and the preserved lateral hypoplastron attributed to "*Trionyx*" cf. *kansaiensis*. It is possible, but not certain, that these elements belong to *Aspideretoides* cf. *riabinini*. If this is the case, then a possible plastral reconstruction has been made to reflect this more extensive lateral development of the plastral callosities (Fig. 2G).

3. Discussion

The examined shell material of trionychids from Dzharakuduk is assigned to *Aspideretoides* cf. *riabinini*, "*Trionyx*" cf. *kansaiensis* and Trionychidae indet. The material referred to Trionychidae indet. may belong to one of the two described trionychid taxa or partially belong to other, unrecognized trionychid taxa. The referral to Trionychidae indet. is not meant to establish the presence of a third taxon, but to present a more accurate picture of the range of morphological variation present in the material from Dzharakuduk even though that variation cannot be easily assigned to a specific taxon.

Aspideretoides cf. *riabinini* belongs to Trionychinae (sensu Meylan, 1987) because it has the nuchal bone that is at least three times wider than long, and a neural series that always contains at least one reversal in neural orientation. This taxon belongs to Trionychini (sensu Meylan, 1987) because it has seven neurals. It is referred to the genus *Aspideretoides* based on its nuchal shape and proportions, the presence of a preneural, and a plastral bridge length greater than one-half hypoplastral maximum length. *Aspideretoides* cf. *riabinini* is very similar to *Aspideretoides riabinini* in the general morphology of the shell elements and sculpture pattern. However, *Aspideretoides* cf. *riabinini* differs from *Aspideretoides riabinini* in its smaller size, slightly greater degree of ossification in the plastron (only in older specimens), a vertical suture between costals 6 and 7 with no underlying costals, and the occasional loss of costals 8. Because these differences may be ontogenetic and/or in need of a confirmation, we refrain from establishing a new species and determine *Aspideretoides* from Dzharakuduk as *Aspideretoides* cf. *riabinini*.

"*Trionyx*" cf. *kansaiensis* is referred to Trionychinae (sensu Meylan, 1987) based on the presence of at least a one reversal in neural orientation. It is similar to "*Trionyx*" *kansaiensis* in the general shape of shell elements and sculpture pattern. In fact, there are no differences between "*Trionyx*" cf. *kansaiensis* and "*Trionyx*" *kansaiensis* other than a smaller size, but "*Trionyx*" cf. *kansaiensis* is so incomplete, that a comparison is not informative. Many parts of the shell, and many potential character differences, are missing.

Thus, our study confirms the presence of at least two shell-based trionychid taxa in Dzharakuduk as suggested by some previous authors (Brinkman et al., 1993; Nessov, 1997). However, our determinations are different. Both of these taxa seem smaller than related trionychids (*Aspideretoides riabinini* and "*Trionyx*" *kansaiensis*) from the Kansai (Tajikistan; Yalovach Formation, lower Santonian) and Shakh Shakh (Kazakhstan; Bostobe Formation, Santonian – lower Campanian) localities (Vitek and Danilov, 2010). However, like in Kansai and Shakh Shakh, in Dzharakuduk the "*Trionyx*" *kansaiensis*-like form is larger than the *Aspideretoides riabinini*-like form. The smaller size may be a true difference between the trionychids of Dzharakuduk and Shakh Shakh, but the smaller size may also be a result of preservation bias. The material from Dzharakuduk is made up of small fragments with very few complete bones, let alone associated bones. Remains of larger trionychids might be present, but too small to be identifiable.

Material of *Aspideretoides riabinini* has been described from the Santonian – ?early Campanian interval of Middle Asia and Kazakhstan. Material of "*Trionyx*" *kansaiensis*, from the Santonian – ?middle Campanian interval of the same region (Vitek and Danilov, 2010, 2012). In addition, *Aspideretoides* sp. was reported from an unknown Late Cretaceous interval of Mongolia (Danilov et al., 2011). Our study expands the geographical and geological distribution of *Aspideretoides* and "*Trionyx*" *kansaiensis*-like trionychids in Asia back to the late Turonian.

Our results improve our understanding of the taxa of Trionychidae within this assemblage as well as similarities and differences between Late Cretaceous turtle assemblages. The turtle assemblage of Dzharakuduk consists of up to seven or eight different taxa (skull-based trionychid taxa are excluded from this count), which represent four families: Adocidae, Lindholmemydidae, Macrobaenidae and Trionychidae (Table 1). This assemblage is most similar to the younger (Santonian – early Campanian) turtle assemblages of Middle Asia and Kazakhstan, namely Kansai and Shakh Shakh (see above), in the presence of the same families and genera, which are *Adocus* and *Shachemys* (Adocidae), *Lindholmemys* (Lindholmemydidae), *Anatolemys* (Macrobaenidae), *Aspideretoides*, *Khunnuchelys* and "*Trionyx*" (Trionychidae). The differences between these turtle assemblages are the following (Table 1): 1) different or potentially different species within some of the genera mentioned above; 2) the presence of a second macrobaenid (Macrobaenidae indet.; = Chelydridae gen. nov.; Nessov, 1997, p. 149; Danilov, unpubl. data) in Dzharakuduk; 3) the presence of "*Paleotrionyx*" *riabinini* in Shakh Shakh, although that taxon is problematic (Vitek and Danilov, 2010); 4) the presence of an unusual trionychid represented by two dentaries in Kansai (Trionychidae indet. 4; Danilov and Vitek, 2012). The Dzharakuduk turtle assemblage also demonstrates some similarities to the turtle assemblage of Kyrkkuduk I (Kazakhstan; Syk-Syuk Formation and, probably, the lower part of the Darbaza Formation, Santonian – ?middle Campanian; see

Table 1
Turtle assemblages from some Late Cretaceous localities of Middle Asia and Kazakhstan. Data about the composition of assemblages are taken from the following publications: Nessov (1997); Vitek and Danilov (2010); Danilov et al. (2011); Vitek and Danilov (2012). See text for other details.

Baybishe and Shakh Shakh	Dzharakuduk	Kansai	Kyrkkuduk I
Adocidae			
Adocus bostobensis	*Adocus aksary*	*Adocus foveatus*	–
Shachemys baibolatica	*Shachemys ancestralis*	*Shachemys baibolatica*	*Shachemys* sp.
Lindholmemydidae			
Lindholmemys sp. cf. *L. gravis*	*Lindholmemys elegans*	*Lindholmemys gravis*	*Lindholmemys* sp.
Macrobaenidae			
Anatolemys maximus	*Anatolemys* sp. cf. *maximus*	*Anatolemys maximus*	–
–	Macrobaenidae indet.	–	–
Trionychidae (shell-based taxa)			
Aspideretoides riabinini	*Aspideretoides* cf. *riabinini*	*Aspideretoides riabinini*	–
"*Trionyx*" *kansaiensis*	"*Trionyx*" cf. *kansaiensis*	"*Trionyx*" *kansaiensis*	"*Trionyx*" *kansaiensis*
"*Paleotrionyx*" *riabinini*	–	–	–
–	Trionychidae indet.	–	Trionychidae indet.
Trionychidae (skull-based taxa)			
Khunnuchelys sp. 1	*Khunnuchelys kizylkumensis*	–	–
–	Trionychini indet.	–	–
–	–	Trionychidae indet. 4	–

Vitek and Danilov, 2012), that includes *Shachemys* sp., *Lindholmemys* sp., "*Trionyx*" *kansaiensis* and the second form of trionychid (Trionychidae indet.). The variations in the trionychid fauna between all of these localities is largely a reflection on the uncertainty surrounding multiple fragmentary remains. The great similarity between these turtle assemblages is explained by their close age and geographical position (late Turonian – ?middle Campanian interval; Middle Asia and Kazakhstan) and corresponds with data from other vertebrates (Averianov and Sues, 2012).

Acknowledgements

We thank the anonymous reviewers whose useful comments improved the quality of this paper. Financial support for our study was provided by a grant from the President of the Russian Federation to the Leading Scientific Schools NSh–6560.2012.4 to I.G.D. This research was supported by the Ministry of Education and Science of the Russian Federation to I.G.D. and a Robert C. Bates travelling fellowship to N.S.V.

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